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APPENDICULAR MYOLOGY, PHYLOGENY, AND CLASSIFICATION OF THE AVIAN ORDER CORACIIFORMES (INCLUDING TROGONIFORMES)

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Abstract

This investigation of phylogenetic relationships in the avian order Coraciiformes addresses the questions of whether the order is monophyletic, whether the individual families are monophyletic, and what the pattern of phylogenetic relationships is among the families. The musculature of the forelimb and hindlimb in 37 species was dissected and variations were used in a cladistic analysis. Monophyly of the order is poorly corroborated but remains the preferred hypothesis based on current knowledge. The classification is based on the phylogeny and all proposed taxa are monophyletic. The order is divided into two suborders. The suborder Coracii contains the families Coraciidae, Brachypteraciidae, and Leptosomidae. The suborder Alcedines is divided into the infraorders Bucerotomorphae and Alcedinomorphae. The Bucerotomorphae contains only the family Bucerotidae, whose division into subfamilies Bucorvinae and Bucerotinae is supported by the results of this study. The infraorder Alcedinomorphae is divided into two subinfraorders. The Upupides include the families Phoeniculidae and Upupidae, whose close relationship is supported by an especially large number of synapomorphies. The subinfraorder Alcedinides includes the superfamilies Momotoidea, containing the Todidae and Momotidae, and Alcedinoidea, including the Meropidae and

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Alcedinidae. The division of the Alcedinidae into subfamilies and tribes offers some confirmation from limb musculature for previous hypotheses of intrafamilial relationships. The present study supports inclusion of the Trogonidae in the Coraciiformes, specifically within the subinfraorder Alcedinides, thus allying the trogons most closely with the assemblage of todies, motmots, bee-eaters, and kingfishers. Uncertainties in the data, however, preclude a more accurate placement of this family relative to the others, so it is listed as *incertae sedis* within the Alcedinides.

INTRODUCTION

This is a study of the phylogenetic relationships in the avain order Coraciiformes based on a cladistic analysis of variations in the muscles of the forelimb and hindlimb. The order as generally recognized (for example, Wetmore, 1960) includes the families Alcedinidae (kingfishers), Todidae (todies), Momotidae (motmots), Meropidae (bee-eaters), Coraciidae (rollers), Brachypteraciidae (ground-rollers), Leptosomidae (formerly Leptosomatidae) (cuckoo-rollers), Upupidae (hoopoes), Phoeniculidae (wood-hoopoes), and Bucerotidae (hornbills). The major questions addressed are these: (1) Is the order Coraciiformes monophyletic? (2) Are the individual families monophyletic? (3) What is the pattern of phylogenetic relationships among the families?

The heterogeneous order Coraciiformes is not easily characterized. Most coraciiforms exhibit syndactyly, a tendency for toes II, III, and IV to be connected basally for part of their lengths, although the details vary in different families. A hallux (digit I) is always present. The palate is desmognathous, with basipterygoid processes rudimentary or absent. The birds included in the order show similarities in formula muscles, pterylosis, and in the frequent possession of brilliant plumages. They are cavity nesters and most species lay from three to six white eggs. The young are nidicolous and naked except in the hoopoes and wood-hoopoes. Most feed on small vertebrates or insects, and the distribution of the order is predominantly in the eastern hemisphere. Part of the problem of defining the group is that there are exceptions to many of the characters that have been used in the past.

The relationships of the Coraciiformes to other birds are obscure, although they are usually regarded as being close to the Passeriformes and Piciformes. A relationship with the trogons (Trogonidae) has been suggested based on overall similarity and derived stapedial morphology (Feduccia, 1975a). Nevertheless, the trogons have generally been placed in an order of their own (Trogoniformes), mostly because of their unique heterodactyl foot structure. The trogons are included in the present study. A thorough review of the taxonomic history of the Coraciiformes and Trogoniformes is provided by Sibley and Ahlquist (1972), so we will merely note at appropriate places a few recent studies of immediate relevance to our work.

MATERIALS AND METHODS

Anatomy

The forelimb and hindlimb muscles of 37 species representing 34 genera in 10 families were dissected with the aid of a stereomicroscope and an iodine muscle stain (Bock and Shear, 1972). For most species only one specimen was dissected. *Coracias benghalensis* was the reference species for which a detailed description of each muscle was written, and against which the homologues in the other species were compared. Among the structural variations in muscles examined were the location and nature of the origin and insertion, the shape of the belly, the fiber architecture of the muscle and the relationship of fibers to tendons, the size of the muscle relative to adjacent structures, and any additional features of note. A large series of drawings of the musculature was made with the aid of a drawing tube attached to the microscope. The present paper is concerned only with a phylogenetic analysis of the forms studied using myological variation as a source of data. The anatomical descriptions and drawings are found in Maurer (1977). Myological nomenclature generally follows the Nomina Anatomica Avium (Baumel et al., 1979).

The following species were dissected (nomenclature from Morony et al., 1975): Alcedinidae, Cerylinae—*Ceryle alcyon, Chloroceryle americana*; Alcedininae—*Alcedo cristata, Ispidina picta, Ceyx argentatus*; Daceloninae—*Pelargopsis capensis, Dacelo guadichaud, Clytoceyx rex, Halcyon smyrnensis, Tanysiptera galatea*; Todidae—*Todus mexicanus, T. subulatus*; Momotidae—*Electron platyrhynchum, Eumomota supercil-iosa, Baryphthengus ruficapillus, Momotus momota*; Meropidae—*Merops hirundineus, M. pusillus, M. albicollis, M. apiaster*; Leptosomidae—*Leptosomus discolor*; Coraci-idae—*Coracias garrulus, C. caudata, C. benghalensis, Eurystomus orientalis*; Upupi-dae—*Upupa epops*; Phoeniculidae—*Phoeniculus bollei, Rhinopomastus cyanomelas*; Bucerotidae—*Tockus erythrorhynchus, Penelopides panini, Aceros undulatus, Anthra-coceros malabaricus, Ceratogymna elata, Bucorvus abyssinicus*; Trogonidae—*Pharo-machrus* sp., *Trogon citreolus, Harpactes erythrocephalus*. No specimens of the Bra-chypteraciidae were available for dissection.

Phylogeny

After the variation in each muscle was recorded, a phylogenetic character analysis was carried out to determine primitive-derived sequences. Kluge (1971), Ross (1974), Hecht and Edwards (1977), and Gaffney (1979) are among the many workers who have discussed these procedures. The basic technique used was outgroup comparison. A character state that occurred both among some members of a presumed monophyletic group and also in outside taxa was considered to be primitive within the clade in question. A variant from this condition that occurred only within the group studied was considered derived within that group. For purposes of comparison with the groups studied herein, we reviewed the conditions in muscles among birds generally, and especially in groups such as the Piciformes and Passeriformes, which are commonly considered to be closely related to the Coraciiformes. These comparative data were taken from George and Berger (1966) and from various investigations underway in our laboratory (for example Borecky, 1977; Bentz, 1979; Raikow, 1978; Swierczewski and Rai-kow, 1981). The data were used to construct a cladogram by clustering taxa into groups through the possession of shared derived character states (synapomorphies) in the usual manner of cladistic analysis.

Classification

A classification of the Coraciiformes was prepared based on the pattern of phyloge-netic relationships hypothesized in the cladogram. It is of the cladistic type in that the

hierarchical structure of the phylogeny is transformed into the hierarchical structure of the classification. Classification has long been a highly subjective procedure lacking in a consistent methodology. We prefer a classification that is internally consistent, and have therefore followed several principles in constructing our classification. There are various approaches to cladistic classification (see Eldredge and Cracraft, 1980, for discussion); ours is based on the following rules:

1) Only clades are classified.—Clades are the products of evolutionary history, while nonmonophyletic groups are simply artifacts of phenetic clustering, adaptational hypotheses, or tradition. Nonmonophyletic groupings may occasionally be useful ("nonpasserines," "birds of prey," "finches") but we see no reason to recognize them as formal taxa.

2) Sister groups are classified at the same category level.—This provides a consistent and pleasing symmetry to the classification by allowing the immediate recognition of sister taxa.

3) Traditional family taxa are maintained.—We comment briefly on subfamily divisions in the Bucerotidae and Alcedinidae, but in general have not attempted to work out the relationships between the genera within families.

4) Nomenclature is conservative.—The names of groups and their category levels are kept as close as possible to previous classifications so as to maximize continuity between classifications.

RESULTS

Our hypothesis of phylogenetic relationships is shown in Fig. 1. Superimposed on this diagram are the taxa that constitute our classification; from this one may see how we derived the classification from the phylogeny. The classification is given in Table 1. Each taxon is hypothesized to be a clade, hence each is an individual hypothesis of monophyly. For each taxon the synapomorphies corroborating the hypothesis are shown alongside the taxon in the classification. In this way the data supporting each component of the total hypothesis are available for examination. The data are given in Table 2. Each character is numbered; these are the numbers referred to in Table 1. The primitive and derived character states are given for each character; the cladogram was of course constructed using the derived states only. For each character, in addition, Table 2 gives the taxa or taxon in which the derived state occurs. Derived states that occur in more than one taxon are hypothesized to have evolved independently in the different groups. In constructing the cladogram we attempted to adhere to the principle of parsimony in minimizing the number of convergent events. With this format our entire argument is set forth unambiguously for maximum ease of understanding and criticism. We regard this as one of the major advantages of cladistic methodology over other approaches to systematic analysis.

The cladogram was generated entirely on the basis of 57 limb muscle characters. We will also discuss some characters used by previous workers, but will not attempt to examine all of the ideas about coraciiform relationships that have been proposed in the past. The following discussion is keyed to the arrangement shown in Fig. 1.
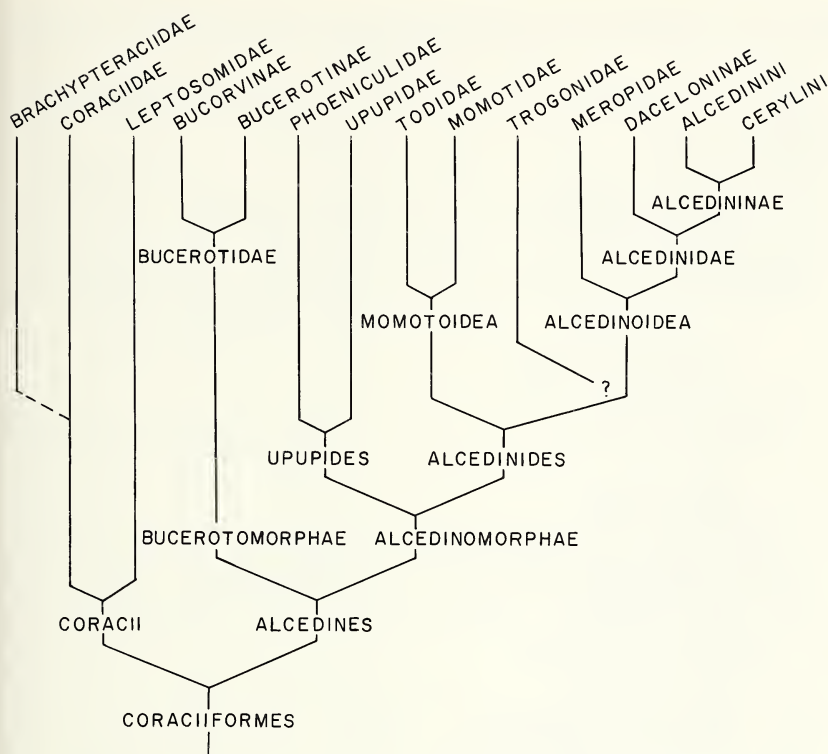
Fig. 1.—A phylogeny of the avian order Coraciiformes. The family Brachypteraciidae was not studied owing to the unavailability of specimens, and is tentatively included here based on previous studies. Otherwise the phylogeny is isomorphic with a cladogram constructed entirely on the basis of a cladistic analysis of 57 limb muscle characters. A proposed higher-level classification is indicated. See Tables 1 and 2 for the data, and the text for discussion.

Coraciiformes

The whole order is clustered by the loss of two muscles, Mm. ambiens and iliofemoralis externus (characters 45, 46, Tables 1 and 2), and by the extensive fusion of the deep plantar tendons (character 53). The latter condition is further modified in some groups. These derived states are among the traditional characters used in defining the order. We did not discover any new limb muscle characters clustering the whole order, and these traditional characters, although sound, are not unique to the Coraciiformes. In addition to the myological characters there are others in osteology, behavior, etc. that have traditionally been used to justify the assemblage (Sibley and Ahlquist, 1972:219).

Table 1.—*A classification of the Coraciiformes with the synapomorphies corroborating each monophyletic taxon.*

Classification	Limb muscle synapomorphies[1]
Order Coraciiformes	45, 46, 53
Suborder Coracii	15, 30
Family Coraciidae	41
Family Brachypteraciidae	(not investigated)
Family Leptosomidae	3, 11, 24
Suborder Alcedines	24, 31, 43
Infraorder Bucerotomorphae	2, 6, 8, 10, 12, 15, 18, 19, 27, 32, 35, 37, 38, 40, 42, 44
Family Bucorvidae	Same as Bucerotomorphae
Subfamily Bucorvinae	34
Subfamily Bucerotinae	5, 23, 26
Infraorder Alcedinomorphae	36, 47
Subinfraorder Upupides	4, 6, 7, 9, 13, 14, 16, 17, 21, 22, 25, 28, 29, 42, 48, 49, 51, 54
Family Phoeniculidae	32
Family Upupidae	37, 55
Subinfraorder Alcedinides	15, 56
Family Trogonidae (*incertae sedis*)	6, 21, 33, 48
Superfamily Momotoidea	25, 48, 49, 50, 51
Family Todidae	20, 37, 39, 41
Family Momotidae	
Superfamily Alcedinoidea	7, 33
Family Meropidae	1, 39, 42, 44, 49, 50
Family Alcedinidae	20, 41, 57
Subfamily Daceloninae	49
Subfamily Alcedininae	48, 51
Tribe Alcedinini	
Tribe Cerylini	49, 52

[1] See Table 2.

These may also be subject to reservations based on occurrence in other groups or exceptions within the Coraciiformes. Sibley and Ahlquist's (1972) study of egg-white proteins was not enlightening with respect to this question.

On the other hand, there is no significant evidence in support of any alternative arrangement. Sibley and Ahlquist (1972:20, 239) suggested a possible connection between the Alcedinidae and the family Galbulidae of the order Piciformes. The results of another investigation in our laboratory (Swierczewski and Raikow, 1981) have led to a rejection of that hypothesis. The ambiguity of the overall coraciiform situation is nicely summarized by the juxtaposition of two quotations from different sections of Sibley and Ahlquist (1972). They consider it "probable" that "the Coraciiformes of Wetmore are polyphyletic" (p. 241), but "resist the temptation to split the order because no compelling

Table 2.—*Characters used in phylogenetic analysis.*

Character	Primitive state	Derived state	Taxa having derived state
1	Latissimus dorsi pars caudalis present	Absent	Meropidae
2	Latissimus dorsi pars caudalis origin more cranial	More caudal	Bucerotomorphae
3	Latissimus dorsi pars caudalis origin limited to neural spines of dorsal vertebrae	Origin also extends to dorsal iliac crest and spinal crest of synsacrum	Leptosomidae
4	Rhomboideus profundus origin from neural spines only	Partial origin from transverse processes	Upupides
5	Rhomboideus profundus with one belly	Two bellies	Bucerotinae
6	Pectoralis pars propatagialis longus fleshy	Tendinous	Bucerotomorphae, Upupides, Trogonidae
7	Tensor propatagialis with one belly	Two bellies	Upupides, Alcedinoidea
8	Tensor propatagialis pars longa present	Absent	Bucerotomorphae
9	Deltoideus major with tendon to latissimus dorsi pars caudalis absent	Present	Upupides
10	Deltoideus major scapular anchor present	Absent	Bucerotomorphae
11	Deltoideus minor insertion cranial to supracoracoideus tendon	Insertion onto supracoracoideus tendon	Leptosomidae
12	As 11	Insertion distal to supracoracoideus tendon	Bucerotomorphae
13	Biceps brachii with 2 tendons of insertion	Three tendons of insertion	Upupides
14	Scapulotriceps with one head	Two heads	Upupides
15	Scapulotriceps humeral anchor present	Absent	Coracii, Bucerotomorphae, Alcedinides[1]

Table 2.—Continued.

Character	Primitive state	Derived state	Taxa having derived state
16	Expansor secundariorum humeral belly present	Absent	Upupides
17	Pronator superficialis insertion semitendinous	Tendinous	Upupides
18	Flexor digitorum profundus with 2 heads	One head	Bucerotomorphae[2]
19	Extensor metacarpi radialis origin by one head	Two heads	Bucerotomorphae
20	Extensor metacarpi ulnaris origin separate from that of ectepicondyloulnaris	Origins fused	Alcedinidae, Todidae
21	Extensor digitorum communis origin from humerus	From humerus and radius	Upupides, Trogonidae
22	Extensor digitorum communis insertion on alular phalanx present	Absent	Upupides
23	Ectepicondyloulnaris origin by one tendon	Two tendons	Bucerotinae
24	Extensor longus digiti majoris pars distalis present	Absent	Alcedines, Leptosomidae
25	Extensor longus alulae radial head present	Absent	Upupides, Momotoidea
26	Extensor longus alulae ulnar head present	Absent	Bucerotinae[3]
27	Interosseus dorsalis bipennate	Unipennate	Bucerotomorphae[4]
28	Interosseus dorsalis present	Absent	Upupides, *Tockus*
29	Interosseus ventralis bipennate	Unipennate	Upupides
30	Iliotibialis lateralis acetabular part fleshy	Aponeurotic	Coracii[5]
31	Iliotibialis lateralis acetabular and postacetabular parts present	Absent	Alcedines, *Eurystomus*

Table 2.—*Continued.*

Character	Primitive state	Derived state	Taxa having derived state
32	Iliotrochantericus caudalis origin from dorsal iliac crest	From spinal crest of synsacrum	Bucerotomorphae, Phoeniculidae
33	Flexor cruris lateralis pars accessoria present	Absent	Trogonidae, Alcedinoidea
34	Flexor cruris lateralis accessory tendon from pars pelvica to femur at insertion of caudofemoralis absent	Present	Bucorvinae
35	Pubo-ischio-femoralis pars medialis undivided	Divided	Bucerotomorphae
36	Pubo-ischio-femoralis bellies separate	Fused	Alcedinomorphae[6], *Eurystomus*
37	Obturatorius lateralis pars dorsalis present	Absent	Bucerotomorphae, Upupidae, Todidae, *Rhinopomastus*
38	Obturatorius medialis oval	Triangular	Bucerotomorphae
39	Gastrocnemius pars medialis (interna) with one head	Two heads	Todidae, Meropidae
40	Gastrocnemius pars medialis (interna) origin from medial surface of tibiotarsus	From caudal surface	Bucerotomorphae
41	Fibularis longus branch to FPD3 tendon present	Absent	Coraciidae, Todidae, Alcedinidae
42	Fibularis longus present	Absent	Bucerotomorphae, Upupides, Meropidae
43	Popliteus present	Absent	Alcedines
44	Plantaris present	Absent	Bucerotomorphae, Meropidae
45	Ambiens present	Absent	Coraciiformes
46	Iliofemoralis externus present	Absent	Coraciiformes
47	Abductor digiti II present	Absent	Alcedinomorphae[1]

Table 2.—*Continued.*

Character	Primitive state	Derived state	Taxa having derived state
48	Adductor digiti II present	Absent	Upupides, Momotoidea, Alcedininae[7], Trogonidae, *Pelargopsis*
49	Extensor brevis digiti III present	Absent	Upupides, Momotoidea, Meropidae, Cerylini, Daceloninae[8], *Corythornis*
50	Extensor brevis digiti IV present	Absent	Momotoidea, Meropidae[9]
51	Abductor digiti IV present	Absent	Upupides, Momotoidea, Alcedininae, *Tanysiptera*
52	Flexor perforatus digiti III—flexor perforatus digiti IV vinculum absent	Present	Cerylini
53	Flexor hallucis longus—flexor digitorum longus tendons not extensively fused	Extensively fused (Gadow's Type V)	Coraciiformes
54	Type V deep plantar tendons present	Flexor hallucis longus alone supplies hallux, with branch to flexor digitorum longus	Upupides
55	Vinculum tendinum flexorum (deep plantar vinculum) present	Absent	Upupidae
56	Flexor hallucis longus supplies hallux	Tendon excluded from hallux	Alcedinides[1]
57	Type V deep plantar tendons	Flexor hallucis longus directly supplies only digits III and IV	Alcedinidae

[1] Except Trogonidae.   [4] Absent in *Tockus*.   [7] Except *Alcedo*.
[2] Except *Anthracoceros*.   [5] Except *Eurystomus*.   [8] Except *Halcyon*.
[3] Except *Tockus*.   [6] Except Todidae.   [9] Except *Merops hirundineus*.

evidence exists to ally any group of the Coraciiformes more closely to a non-coraciiform than to other members of the Coraciiformes'' (p. 230).

In short, there is a fair amount of rather circumstantial evidence in support of coraciiform monophyly and no significant argument against it. We will therefore proceed on the working assumption that the monophyly of the order Coraciiformes is the best hypothesis at the present state of our knowledge.

Coracii

The rollers and cuckoo-rollers, Coraciidae and Leptosomidae, appear to form a relatively primitive group, lacking many derived myological states found in the remaining families. The group is defined cladistically by the scapulotriceps humeral anchor (character 15) and the aponeurotic acetabular part of M. iliotibialis lateralis (character 30). Because the first of these occurs in several groups, it is a weak character. The grouping is supported by a series of skull characters and certain aspects of the postcranial skeleton (Cracraft, 1971).

No specimens of the family Brachypteraciidae were examined in the present study. It is tentatively placed next to the Coraciidae in our diagram on the recommendation of Cracraft (1971). The Coraciidae are set apart from the Leptosomidae by character 41. The Leptosomidae are set apart from the Coraciidae by derived states 3, 11, and 24. Two of these are unique and attest to the distinctiveness of this family. Additionally, the Leptosomidae are defined by osteological traits (Cracraft, 1971) and by other traits that are almost certainly derived within the order—a powder down patch, a semi-zygodactyl foot, and a bronchial syrinx (Sclater, 1865).

Alcedines

The remaining families are clustered by muscular reductions and losses (characters 24, 31, 43). Additionally M. fibularis longus is reduced in all except the Momotidae and Trogonidae, but it is unclear whether this muscle is independently reduced in the various families or whether the condition in the motmots and trogons is an evolutionary reversal.

Bucerotomorphae

The hornbills (Bucerotidae) form a highly distinctive group with sixteen derived states, most of which are unique, in their limb muscles (Tables 1, 2). Two groups may be recognized that correspond to Bannerman's (1933) subfamilies. These are the Bucorvinae, containing only the ground hornbills of the genus *Bucorvus,* and the Bucerotinae, including all other forms. The Bucorvinae are clustered by a special-

ization of the flexor cruris lateralis (34) and by terrestrial habits, which would appear to be derived within this mostly arboreal order of birds. The Bucerotinae have several derived states separating them from the Bucorvinae (5, 23, 26), and in addition, it appears certain that the remarkable walling-up nesting behavior of the former is also a synapomorphy of the subfamily. Kemp (1979) presented a different view of hornbill phylogeny, in which *Bucorvus* is considered to be a phyletically advanced genus rather than being the sister group of all the other genera as suggested here. We prefer our hypothesis because Kemp's is based largely on behavioral characteristics about which he himself expresses uncertainty, and because his cladogram includes several clades for which he provides no defining characters.

Alcedinomorphae

This cluster is only weakly defined by limb myology. There are two derived states, but each has an exception (Tables 1, 2). The bellies of M. pubo-ischio-femoralis are fused (also in *Eurystomus*) (character 36), and the adductor digiti II is lost (47) except in the Trogonidae.

Upupides

The generally accepted idea of a close relationship between the hoopoes and wood-hoopoes is strongly corroborated by the limb musculature, with 18 synapomorphies (Nos. 4, 6, 7, 9, 13, 14, 16, 17, 21, 22, 25, 28, 29, 42, 48, 49, 51, 54), in addition to which each family is distinguished from the other (Tables 1, 2). Feduccia (1975b) hypothesized a similar relationship between the Upupidae and Phoeniculidae on the basis of a derived "anvil" stapes morphology.

Alcedinides

This group, including the Todidae, Momotidae, Meropidae, Alcedinidae, and Trogonidae, corresponds to the "Alcediniform assemblage" that Feduccia (1975a) defined on the basis of a derived morphology of the stapes. The first four families are clustered by characters 15 and 56, and by being tunnel nesters and having similar egg-white patterns (Sibley and Ahlquist, 1972), but the trogons do not fit with these characteristics (see below).

Momotoidea

The todies and motmots, Todidae and Momotidae, are shown to be sister groups by five synapomorphies (25, 48, 49, 50, 51; Tables 1, 2). Olson (1976) provided osteological and paleontological evidence that the todies are descended from a momotid-like ancestor. Kepler (1977) linked todies and motmots by morphological, behavioral, and developmental characteristics. The Momotidae are not further distinguished

by derived myological characteristics, but that the Todidae are the more highly advanced of the two families is shown by several additional synapomorphies (20, 37, 39, 41; Tables 1, 2).

Alcedinoidea

The bee-eaters and kingfishers, Meropidae and Alcedinidae, are shown to be sister groups by two apomorphic muscular characters (7, 33), the latter also shared with the trogons, discussed below. The two families are each further defined as separate monophyletic groups by the possession of additional synapomorphies (Tables 1, 2). Within the Alcedinidae some separation into groups of genera corresponding to recognized subfamilies is provided by limb muscle characters, which support the general picture that the forest kingfishers (Daceloninae) are more primitive than the fishing kingfishers (Alcedininae). The latter group is sometimes separated into two subfamilies. There is some suggestion of support for this division (here into tribes Alcedinini and Cerylini) from the limb muscles, but the data are not unequivocal. Because this is such a large and diverse family, and because we dissected a relatively few forms, we emphasize the need for more comprehensive studies of the kingfishers. Fry (1980) has recently reviewed the family.

Trogonidae

This family has long been a taxonomic puzzle, its relationships having been much debated (Sibley and Ahlquist, 1972:213–218). It is generally agreed that the trogons are probably close to the Coraciiformes. Their distinctiveness has been emphasized perhaps excessively by the uniquely derived condition of their heterodactyl foot, a perching adaptation in which digits I and II are directed backward in opposition to III and IV. In the most recent attempt to clarify the relationship of trogons, Feduccia (1975a) made a cladistic analysis of the stapes (middle ear ossicle) and allied the trogons with the Todidae, Momotidae, Meropidae, and Alcedinidae in an order "Alcediniformes," which corresponds to our subinfraorder Alcedinides.

What does the limb musculature contribute to the hypotheses that the trogons are coraciiform, and more specifically, part of the Alcedinides? The trogons share characters 45 and 46 with the Coraciiformes. They differ, however, in no. 53, having Gadow's type VIII deep plantar tendon arrangement rather than type V. We consider it possible that this autapomorphous condition evolved from the type V arrangement by a partial rearrangement of the distal ends of the tendons of the flexor hallucis longus (FHL) and flexor digitorum longus (FDL). Such rearrangements are common among birds; for example, a more complex one than that suggested here occurred in the evolution

of the Piciformes (Swierczewski and Raikow, 1981). Following Gadow, a hypothesis for the evolution of the arrangement of the deep plantar tendons of the trogons from the primitive coraciiform condition is shown in Fig. 2 (see Gadow, 1894:617). Fig. 2A shows the condition (Gadow's type V) found in the Coraciidae, Leptosomidae, and Bucerotidae, that we believe to be primitive in the Coraciiformes (but derived in the class Aves). In this arrangement the two deep flexor tendons fuse and then bifurcate, one branch supplying the hallux, the other subsequently dividing to supply digits II, III, and IV. Fig. 2C shows the condition found in trogons (Gadow's type VIII). FHL supplies digits I and II, and FDL supplies III and IV. A vinculum (v) connects the two. The speculative diagram in Fig. 2B shows how the trogon condition could have evolved from the primitive coraciiform condition. At (a) separation of the coalesced tendons would have occurred, whereas at (b) a division would have arisen. The vinculum would be the remnant of the formerly extensive connection. Presumably this change would have occurred by a modification in embryonic development, possibly involving changes in tendon fiber orientation associated with modified tensional forces resulting from the shifted position of the second digit. Such a modification would give the unique trogon arrangement in which the tendon of the FHL supplies digits I and II, while the tendon of the FDL supplies digits III and IV. This symmetrical distribution of tendons is obviously a functional correlate of the heterodactyl foot, providing a balanced distribution of muscle force to the two opposing pairs of toes. The toe arrangement and tendon arrangement are thus parts of a single derived functional specialization, autapomorphic for the Trogonidae, and need not be considered a refutation of the hypothesis that the trogons are coraciiform.

The Alcedines are defined by characters 21, 34, and 43, with which the trogons are in agreement. The Alcedinomorphae are defined by character 36, with which the trogons agree, and 47, with which they do not. Character 47 is the loss of the abductor digiti II, a small intrinsic foot muscle that is retained by trogons. This argues against Feduccia's and our hypothesis. However, the loss of small toe muscles is a frequent occurrence in birds, and it is possible that this muscle was lost independently in several groups, but we have no way to decide this.

The Alcedinides, corresponding to Feduccia's Alcediniformes, are clustered by characters 15 and 56, with which the trogons do not conform. Character 56 is perhaps not important; a feature of the deep plantar tendons, its modification in trogons could be part of the change associated with heterodactyly.

There is finally the irksome question of why heterodactyly should arise in a group situated in the midst of an assemblage of syndactyl
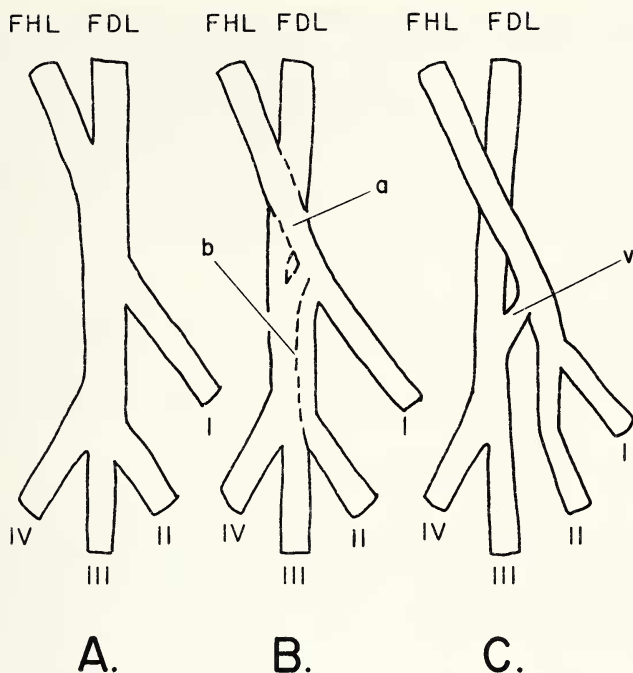
Fig. 2.—A hypothesis for the evolution of the unique arrangement of the deep plantar tendons in trogons. In A is shown the arrangement believed to be primitive within the Coraciiformes, whereas in C is shown the arrangement found in trogons. B shows a speculative diagram indicating changes that could have occurred in A to give C. See text for discussion. Abbreviations: FHL, tendon of M. flexor hallucis longus; FDL, tendon of M. flexor digitorum longus; a, area of separation of coalesced tendons; b, line along which tendon splits apart; v., vinculum; I, II, III, IV, numbers of digits.

forms, as the two conditions are regarded as alternative perching specializations. Bock and Miller (1959) consider syndactyly to be a perching adaptation in which the binding together of the forward toes holds them at right angles to the branch, providing a maximally efficient grip. They consider heterodactyly an alternative solution to the problem of evolving an effective perching foot. It therefore seems more likely that the heterodactyl foot evolved from an anisodactyl condition than from a syndactyl condition. Extreme syndactyly may also be functionally significant in digging, and the possibility exists that syndactyly arose independently in the various coraciiform groups.

On the basis of the above discussion of limb muscle characteristics, we feel that the family Trogonidae is reasonably included in the order Coraciiformes, and in the subinfraorder Alcedinides. The peculiarities

of its hindlimb muscles may well be associated with the evolution of the heterodactyl foot, but because they are apomorphic we cannot determine the sister taxon of the Trogonidae using myological characters, and therefore in our classification we have listed it as *incertae sedis* within the Alcedinides. The placement of the Trogonidae in the cladogram (Fig. 1) is suggested by character 33, which links the Meropidae, Alcedinidae, and Trogonidae, but because of the other problematical characters this placement is highly tentative.

DISCUSSION

Some characters suggest alternative clustering arrangements, but we have chosen the hypothesis that minimizes the number of independent origins of derived states, and which seems to us to be the most consistent with the data analyzed in the context of our general understanding of the overall problem. The degree of confidence that each individual hypothesis of monophyly generates will depend in part on the number and kind of characters supporting it. These points are discussed more fully elsewhere (Swierczewski and Raikow, 1981).

The hypothesis of coraciiform monophyly is not strongly corroborated by present information. Although there are several derived states clustering the group, these also occur in other birds and could as well have been derived at a higher level within the class Aves as at the level postulated herein. The ambiens (45) is also, for instance, absent in the Piciformes and Passeriformes. The iliofemoralis externus (46) is similarly absent in the Piciformes and in most Passeriformes, and its presence in a few members of the latter group is believed to be a secondary reoccurrence (Raikow et al., 1979). Thus these characters could well define a cluster consisting of these three orders, whose close affinity is generally admitted. However, both the Piciformes and Passeriformes are well-defined clades (Swierczewski and Raikow, 1981; Raikow, in preparation), so that this hypothesis would still leave two possibilities—the Coraciiformes could constitute a nonmonophyletic group within the larger clade (like the "reptiles" within the clade Amniota), or it could be monophyletic as defined by character 53, extensive fusion of the deep plantar tendons. Speculations along these lines could be extended at great length but to no useful purpose. On the basis of present understanding we feel it best to proceed with a hypothesis of coraciiform monophyly, with the recognition that future studies providing *new data* might well necessitate the abandonment of that position.

CONCLUSION

The phylogeny developed in this study entirely on the basis of data from one system, the limb muscles, correlates well with previous

workers' conclusions based on other data. Feduccia's hypothesis of the monophyly of the Alcediniformes (our Alcedinides) is supported, as is his contention that the Trogonidae are part of that assemblage. The exact position of the Trogonidae remains uncertain, however. The idea that the traditional families of the Coraciiformes are each mono-phyletic is upheld in most cases by derived conditions in their limb myology. Monophyly of the hornbills and of the hoopoe/wood-hoopoe assemblages are especially well corroborated. In contrast, the mono-phyly of the Coraciiformes as a whole, and of some clades within it, are much less strongly supported. Our study appears to be the most thorough that has been made of this group, and we consider that our phylogeny and the classification derived from it are the most solidly documented studies to date of this most troublesome group of birds, but future studies will no doubt lead to further clarification of the problem.

ACKNOWLEDGMENTS

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